

## Three New Records of Indo-West Pacific Littorinidae (Gastropoda) in the Tropical Eastern Pacific

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**Abstract.** Three species of Littorinidae that are widespread in the Indo-West Pacific (IWP) region are recorded from the Tropical Eastern Pacific (TEP) for the first time: *Littoraria indulata* (Gray, 1839) on Isla del Coco, *L. coccinea* (Gmelin, 1791) on Isla del Coco and Clipperton Atoll, and *Peasiella conoidalis* (Pease, 1868) on the mainland of Costa Rica. These are briefly described and figured. It is suggested that these may have been transported to the TEP as pelagic eggs or larvae, carried on the North Equatorial Countercurrent, perhaps during the enhanced flow characteristic of El Niño events. Records of IWP mollusks in the TEP are reviewed and reasons for the general lack of established populations of these species are discussed.

### INTRODUCTION

The marine zoogeographic region of the Tropical Eastern Pacific (TEP) is separated from that of the Indo-West Pacific (IWP) by more than 5000 km of open ocean. Lacking islands as stepping stones, this expanse of deep ocean provides an obstacle to the trans-Pacific dispersal of shallow-water organisms and has been termed the "Eastern Pacific Barrier" (EPB; Ekman, 1953). The EPB is widely acknowledged as the most effective marine barrier to the dispersal of tropical shelf invertebrates in the modern oceans and throughout the Cenozoic (Grigg & Hey, 1992). Nevertheless, there is increasing evidence that the EPB is by no means impassable and that it in fact acts more as a filter bridge than a barrier, since some species are found on both sides. Compilations of these trans-Pacific distributions have been made for various animal groups including corals (Glynn & Ault, 2000), echinoderms (Lessios, et al., 1996), shorefishes (Robertson & Allen, 1996), and mollusks (Emerson, 1991; Emerson & Chaney, 1995). In nearly all of these cases, the TEP records have been explained by relatively recent dispersal from the IWP to the east; only in the case of a few shorefishes are there clear examples of TEP endemics that have crossed the barrier in the reverse direction (Robertson & Allen, 1996). An alternative interpretation is that trans-Pacific distributions are of more ancient origin, representing relicts of previously continuous Tethyan distri-

butions that were separated by vicariance as the EPB developed (McCoy & Heck, 1976; Heck & McCoy, 1978; Rowe, 1985). For a small number of invertebrate species there is now molecular evidence to support the dispersalist interpretation that disjunct populations of trans-Pacific species have indeed been connected by recent gene flow, and are not ancient isolates (Lessios, et al., 1998).

The causes of the apparent asymmetry of dispersal of tropical shallow-water invertebrates across the EPB are debated and may involve both current patterns and ecological factors (Scheltema, 1988; Grigg & Hey, 1992). Currents that are believed to transport larvae and propagules across the Pacific flow in both directions, but show seasonal variation in intensity and composition, so that prediction of their influence on dispersal is difficult. Those flowing westward are the North Equatorial and South Equatorial Currents, originating in the temperate Californian and Peruvian biogeographic provinces respectively; it has been claimed that these are too cool to be vehicles for tropical Panamic species (Zinsmeister & Emerson, 1979), but they do in fact contain a component of tropical water (Scheltema, 1988). The major warm-water currents traversing the EPB flow along and north of the Equator in an eastward direction, the North Equatorial Countercurrent (NECC) and cooler subsurface Equatorial Undercurrent. The source area for IWP immigrants to the TEP is generally considered to be the Line Islands, since the most direct route across the EPB is the 5400 km from Christmas Island to Clipperton Atoll in the path of the eastward flowing NECC (Richmond, 1990; Finet, 1991; Grigg & Hey, 1992). This is a seasonal cur-

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rent, flowing from May to December, and during normal years the time taken to cross the EPB has been estimated at a mean of 155 days, or as little as 100 days (Richmond, 1990). However, this time may be reduced to only 50–60 days during periodic El Niño-Southern Oscillation (ENSO) events, when the rate of eastward surface flow and latitudinal extent of the current are increased (Richmond, 1990; Glynn et al., 1996). ENSO events occur every four to nine years, with unusually strong episodes once or twice in a century (Grigg & Hey, 1992). Although few long-term records are available, it has been noticed that new and infrequent records of IWP species in the TEP frequently coincide with or immediately follow strong ENSO events (Kay, 1991; Emerson & Chaney, 1995; Lessios et al., 1996, 1998; Robertson & Allen, 1996).

Mollusks provide especially clear examples of trans-Pacific migrants and the influence of ENSO events, since they are thoroughly collected, geographical ranges are relatively precisely known, life histories are often understood, and larvae have been recorded in oceanic currents. The gastropod species of IWP origin that have been recorded in the TEP have been reviewed most recently by Emerson (1991) and the Cypraeidae by Emerson & Chaney (1995). In addition to the references cited by these authors, further records have been added, and in some cases removed, by others (Shasky, 1983, 1986, 1987a,b, 1988, 1995; Kay, 1991; Emerson, 1993, 1994, 1995, 1999; Chaney, 1996; Hollmann, 1996; Kaiser, 1997, 1998, 1999; Hertz & Kaiser, 1998; Reid, 1999a). Those presumed to be of natural occurrence (rather than human introduction) consist of 77 species (excluding cases recognized as subspecifically distinct). Of these trans-Pacific taxa, 14 are tonnoideans, many of which have distributions throughout the worldwide tropics and are known to be widely dispersed by means of exceptionally long lived teleplanic larvae (Scheltema, 1988). The remainder are mostly members of the Cypraeidae (12 species, Emerson & Chaney, 1995) and Neogastropoda (32 species). Of the non-tonnoideans the great majority represent rare occurrences rather than established populations, and about 60% of them are recorded only from the islands of the TEP and not from the American mainland (Emerson, 1991). Of the few that maintain viable, self-sustaining populations in the TEP, two are considered sufficiently distinct morphologically from IWP populations that they are accorded the status of subspecies (Vermeij, 1990; Reid, 1999a). Three additional species have been interpreted as TEP endemic species with a recent ancestry in the IWP (Vermeij, 1990).

The family Littorinidae is one of the most thoroughly studied among marine gastropods; its taxonomy is largely resolved, and both distribution and larval development are known for most species (e.g., Rosewater, 1970; Reid, 1986, 1989a,b, 1999a; Reid & Mak, 1998). The littorinid fauna of the TEP (from the Gulf of California to north-

ernmost Peru) is being revised and is presently known to consist of six species of *Littoraria* (Reid, 1999a), 15 of *Nodilittorina* (Reid, in preparation), and a species introduced from the western Atlantic (*Cenchritis muricatus* [Linnaeus, 1758]; Bishop, 1992; Chaney, 1992). Of these species, only one, *Littoraria pintado* (Wood, 1828), is known to have a trans-Pacific distribution, and the populations in the TEP are classified as an endemic subspecies, *L. pintado pullata* (Carpenter, 1864) on account of their consistently darker shells (Reid, 1999a). Among trans-Pacific gastropods this species is unusual in several respects. The TEP populations are restricted to Isla del Coco (Cocos Island), Clipperton Atoll, the Revillagigedo Islands, southern Baja California, and a few isolated occurrences on the southern mainland of Mexico. At least on the islands and in Baja California, the populations are large, clearly self sustaining, and not dependent upon immigration from the IWP. (To these records can be added a single live-collected specimen of *L. pintado pullata* from the Isla de Malpelo, Colombia; leg. K. L. Kaiser, 30 March 1998; K. L. Kaiser Collection.) Reid (1999a) argued that since the closest IWP occurrences are in the Hawaiian Islands, rather than in the traditional source area of the Line Islands, it is likely that there is at present no genetic contact between the two subspecies, even during exceptional ENSO events. There is one other record of an IWP *Littoraria* in the TEP, based on a single shell of *L. intermedia* (Philippi, 1846) from the Galápagos Islands (Wreck Bay, Chatham Island, 1937, G. Vanderbilt Collection, ANSP 170348; Reid, 1986). This occurrence has not been confirmed and is considered unreliable; Reid (1986) regarded the record as doubtful (see also remarks in Systematic Descriptions below on an unreliable collection of *Littoraria coccinea* from the same source).

In the course of the study of the littorinids of the eastern Pacific, three IWP littorinids new to the fauna of the TEP have been found and are recorded here.

## MATERIALS AND METHODS

Approximately 1000 lots of littorinids from the TEP have been examined, including both personal collections and material in major museums (Natural History Museum, London, BMNH; National Museum of Natural History, Washington, D.C., USNM; Natural History Museum of Los Angeles County, LACM; Muséum National d'Histoire Naturelle, Paris, MNHN; additional material from the Academy of Natural Sciences of Philadelphia, ANSP; Museum of Comparative Zoology, Harvard; California Academy of Sciences, CAS; Santa Barbara Museum of Natural History, SBMNH). In addition, the faunistic literature on the TEP has been thoroughly checked. In the following descriptions only brief synonymies are given, indicating references to recent taxonomic accounts.



Figure 1. Map of new records of Indo-West Pacific Littorinidae in tropical eastern Pacific: *Littoraria undulata* (triangle), *L. coccinea* (circles), and *Peasiella conoidalis* (asterisk).

## SYSTEMATIC DESCRIPTIONS

### *Littoraria* (*Protolittoraria*) *undulata* (Gray, 1839)

(Figure 2A)

*Littorina undulata* Gray, 1839:140 (lectotype BMNH 1968362; Okinawa, Ryukyu Islands; lectotype and type locality designated by Rosewater, 1970).

*Littorina* (*Littoraria*) *undulata* Rosewater, 1970:436–439 (includes synonymy), pl. 325, figs. 8–10, pl. 332, pl. 333 (radula, penis, egg capsule).

*Littoraria* (*Littoraria*) *undulata* Reid, 1986:73, figs. 4e (penis), 99 a–c. Reid, 1992:195, figs. 1d (penis), 2d (oviduct), pl. 4c, d.

*Littoraria undulata* Reid & Mak, 1999:figs. 3G, H (radula). *Littoraria* (*Protolittoraria*) *undulata* Reid, 1999b:310.

**Diagnosis:** Shell height to 26 mm, solid, height/breadth ratio = 1.45–1.71; columella long, straight, wide; sculpture of 7–10 primary grooves on spire whorls, increasing

to 22–36 (rarely to 53) incised lines on last whorl, but sculpture sometimes faint; color variable, whitish, grey or pink, with spots, axial streaks or marbled pattern of dark or red brown, often forming 8–14 zigzag or axial lines on last whorl, columella lilac. Penis with bifurcate base, short filament less than half length of wrinkled base, sperm groove open; very large glandular disc. Pallial oviduct a single spiral of albumen and capsule glands, 5.5 whorls. (After Reid, 1992.)

**Record in TEP (Figure 1):** One live specimen, Bahía Wafer, Isla del Coco, Costa Rica, 26 May 1985, leg. K.L. Kaiser, SBMNH 345468 (Figure 2A).

**Remarks:** This species occurs on a range of substrates in the littoral fringe, including basalt, limestone, beach-rock, concrete, driftwood, and (rarely) mangroves, both on oceanic islands and continental shores (although it is absent in turbid situations). It is one of the most wide-



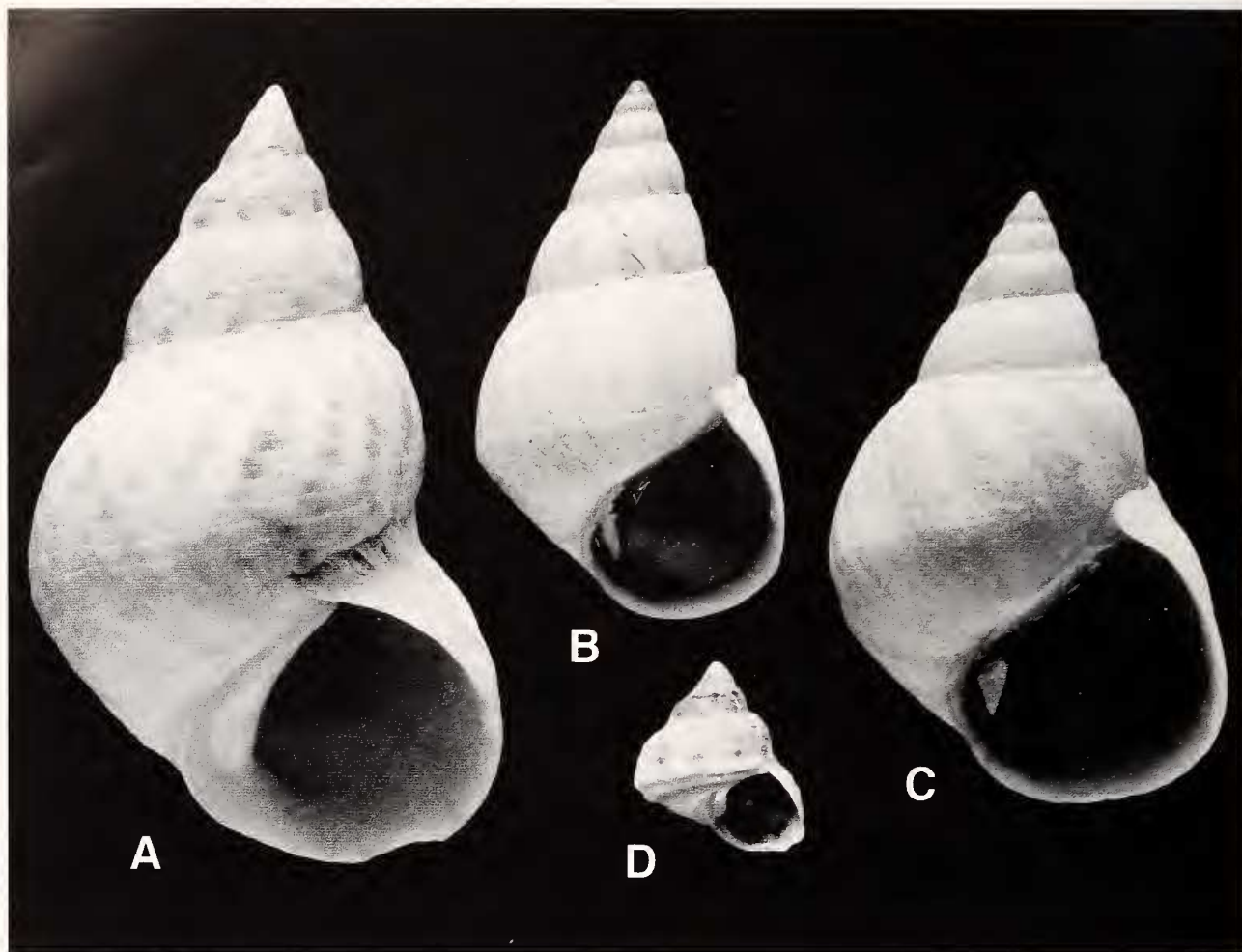


Figure 2. Shells of Indo-West Pacific Littorinidae newly recorded in the Tropical Eastern Pacific. A. *Littoraria undulata* (23.7 mm; Bahía Wafer, Isla del Coco, Costa Rica; SBMNH 345468). B. *Littoraria coccinea* (16.1 mm; SE corner Clipperton Atoll; SBMNH 345467). C. *Littoraria coccinea* (19.3 mm; Bahía Chatham, Isla del Coco, Costa Rica; SBMNH 345466). D. *Peasiella conoidalis* (1.1 mm diameter; off Bahía Herradura, Puntarenas Province, Costa Rica; LACM 72-54).

spread of IWP littorinids, from South Africa (Kilburn, 1972), India, Indonesia, Australia, and all across the western Pacific to Hawaii and Palmyra in the Line Islands (Rosewater, 1970: pl. 334), including Hong Kong (Reid, 1992), but excluding Polynesia. The pelagic egg capsule has been described (Rosewater, 1970: pl. 333, figs. C, D), and like all but one of its congeners it undoubtedly undergoes planktotrophic development (Reid, 1989a).

In shape, the shell shows some similarity to that of *Littoraria pintado pullata* (see Reid, 1999a), but in that species the coloration is blackish or dark brown, with a pattern of dense dots or spiral lines, and the columella is white edged with brown. Also similar is the shell of *L. rosewateri* Reid, 1999 (see Reid, 1999a: figs. 9A–D), but with a smaller, taller shell and a short columella; that species is restricted to mangrove, salt marsh, and muddy habitats on mainland shores from Mexico to Ecuador. The

shell of *L. undulata* is distinguished from that of the other rare IWP immigrant *L. coccinea* by its stronger sculpture, long lilac columella, and brown pattern; penial shapes are also diagnostic.

*Littoraria* (*Protolittoraria*) *coccinea* (Gmelin, 1791)

(Figures 2B, C)

*Helix coccinea* Gmelin, 1791:3651 (lectotype figure Martyn *Universal Conchologist* vol. 2, pl. 68, left external figure; Tahiti; lectotype and type locality designated by Rosewater, 1970).

*Littorina* (*Littoraria*) *coccinea* Rosewater, 1970:439–441 (includes synonymy), pl. 325, figs. 11, 12, pl. 335, pl. 336 (radula, penis, egg capsule).

*Littoraria* (*Littoraria*) *coccinea* Reid, 1986:73, fig. 4b (penis).

*Littoraria coccinea* Reid & Mak, 1999: figs. 3A, B (radula).

*Littoraria (Protolittoraria) coccinea* Reid, 1999b:310, fig. 1H (egg capsule).

**Diagnosis:** Shell height to 29 mm, solid, height/breadth ratio = 1.40–1.64; columella short; sculpture of 8–10 primary grooves on spire whorls, usually becoming obsolete on last whorl leaving a smooth glossy surface; color whitish, with pink peripheral band, darker on spire whorls, pink growth lines on last whorl, columella and aperture dark orange, columella usually tinged with purplish brown. Penis with bifurcate base, long vermiform filament two to three times length of wrinkled base, sperm groove open; moderately large glandular disc. Pallial oviduct a single spiral of albumen and capsule glands, 5.5 whorls.

**Records in TEP (Figure 1):** Three live specimens, Bahía Chatham, Isla del Coco, Costa Rica, 23 May 1985, leg. K.L. Kaiser, SBMNH 345466 (Figure 2C); one live specimen, SE corner Clipperton Atoll, 28 April 1998, leg. K.L. Kaiser, SBMNH 345467 (Figure 2B). One lot of 16 specimens from Wreck Bay, Chatham Island, Galápagos Islands (leg. R.W. Smith, 1931, G. Vanderbilt Collection, ANSP 170347) is considered unreliable. This is because the sample is remarkably large for a rare immigrant species. Furthermore, the following lot in the ANSP registration sequence is a shell of another IWP species, *Littoraria intermedia*, said to be from the same locality (see Introduction above). This coincidence is likely the result of mislabelling.

**Remarks:** This species is likewise found on a range of substrates in the littoral fringe, including basalt, concrete, limestone, and driftwood, but is restricted to islands and shores with clear oceanic water. It is largely confined to the western Pacific, from the Ryukyu Islands and the Philippines across Oceania to Hawaii, the Line Islands and Polynesia, and including islands of the Australian Barrier Reef (Rosewater, 1970: pl. 337). There is one record from the Cocos-Keeling Islands in the Indian Ocean (Rosewater, 1970; DGR personal observation of USNM 589143); here, as elsewhere in the Indian Ocean, the more common species is *L. glabrata* (Philippi, 1846), sister species of *L. coccinea*. The egg capsule has been figured by Rosewater (1970) and Reid (1999b), and the species undoubtedly undergoes planktotrophic development (Reid, 1989a).

Its smooth, pinkish-white, orange-mouthed shell is highly distinctive and should not be confused with that of any other species in the TEP. The lack of dark color pattern, short columella without lilac color, and virtually smooth shell distinguish this species from the other IWP immigrant, *L. undulata*.

*Peasiella conoidalis* (Pease, 1868)

(Figure 2D)

*Trochus conoidalis* Pease, 1868:287, pl. 24, fig. 8 (4 syn-types ANSP 18868; Paumotu [= Tuamotu Islands]).

*Peasiella conoidalis* Reid, 1989b:55–56 (includes synonymy), figs. 2, 16, 18 (protoconch), 23–24 (radula), 37–38 (penis), 74–81. Reid & Mak, 1998:26–28, figs. 138–141.

**Diagnosis:** Shell to 5 mm diameter, trochoidal, height/breadth ratio = 0.77–1.33; periphery strongly keeled with a straight or crenulated flange; small open umbilicus; sculpture of 4–12 grooves above periphery, 4–8 ribs on base; color white to yellow with minute brown dots or lines in grooves. Operculum corneous, multispiral. Penis long, vermiform, with closed sperm groove; single mammilliform penial gland at half length of penis. Pallial oviduct a backward loop of albumen gland followed by larger loop of capsule gland; copulatory bursa absent. (After Reid, 1989b.)

**Record in TEP (Figure 1):** One dead specimen, 20 fathoms (37 m), off Bahía Herradura, Puntarenas Province, Costa Rica, 10 March 1972, leg. McLean & Bussing, RV *Searcher*; LACM 72–54 (Figure 2D).

**Remarks:** The habitat of this species is lower on the shore than that of the larger littorinids, and it can be found among coral rubble on intertidal reef flats and among barnacles on beachrock, mainly on atolls and oceanic islands (Reid, 1989b). The recorded shell was dead collected, and the depth of 37 m is well outside its known intertidal habitat. Its distribution is wide, stretching from Kenya to southern Japan, northeastern Australia and across the Pacific to the Line Islands and Polynesia (Reid, 1989b; Reid & Mak, 1998). All known species of *Peasiella* possess a large capsule gland in the pallial oviduct and a protoconch that indicates planktotrophic development (Reid, 1989a, b); the pelagic egg capsules of several species have been described (Reid & Mak, 1998).

This is the first record of the Indo-West Pacific genus *Peasiella* in the TEP. The generic name was used for a new species, *Peasiella roosevelti*, described from the Galápagos by Bartsch & Rehder (1939), but that has been shown to be a synonym of *Nodilittorina porcata* (Philippi, 1846) (Reid, 1989a). Confusion of this with other littorinid species in the TEP is unlikely; the only species with similarly small umbilicate shells are members of the *Nodilittorina porcata* complex, but in those the outline is globular or carinate, rather than trochoidal, and there is often a coarse black color pattern. It is, however, possible that specimens of *P. conoidalis* may be misidentified as members of the Trochidae, and in such cases may have been overlooked in museum collections.

## DISCUSSION

We have reported the occurrence of three IWP littorinids in the TEP, *Littoraria undulata* on Isla del Coco, *L. coccinea* on Isla del Coco and Clipperton Atoll, and *Peasiella conoidalis* on the mainland of Costa Rica (Figure 1). The last of these is a minute species that might hith-



erto have been overlooked or misidentified, but the two *Littoraria* species are large, distinctive, and easily collected in their high intertidal habitat. Neither was listed from Clipperton Atoll by Emerson (1994) nor from Cocos Island by Montoya (1983). All these new records fit the typical profile of most of the known records of IWP non-tonnoidean gastropod species in the TEP (Emerson, 1991): the species are widespread in the IWP (including the Line Islands) and of rare occurrence in the TEP, they have planktotrophic development and therefore the potential for dispersal in ocean currents, and (with the exception of *P. conoidalis*) they have been discovered on the oceanic islands of the TEP in the path of the eastward-flowing North Equatorial Countercurrent. It has been suggested that transport of IWP species to the TEP is more likely during ENSO events (Richmond, 1990), so it is interesting that the collections of living *Littoraria* were made during or shortly after the strong ENSO events of 1982–1983 and 1997–1998 (precise growth rate data are not available for these species, but in the case of the 1985 collections survival for 2–3 years is possible).

The means of transport of these species to the TEP can only be a matter of speculation. There is no doubt that all have pelagic eggs and planktotrophic development, but the length of larval life is unknown. The only tropical littorinid to have been successfully reared to metamorphosis is *Nodilittorina hawaiiensis* Rosewater & Kadolsky, 1981, which settled 3–4 weeks from spawning (Struhsaker & Costlow, 1968, as *Littorina picta*). A similar length of pelagic life can be predicted for the present species on the basis of similarity of egg size and protoconch. This length of time is still much less than the minimum estimate of 50–60 days to cross from the Line Islands to Clipperton Atoll in the NECC during peak flow at a time of an ENSO event (Richmond, 1990; Glynn et al., 1996). Still faster transport may be possible, as suggested by settlement in the TEP of the IWP coral *Acropora* with a larval competency period of less than 25 days (Richmond, 1990). It is also possible that larval competency of these littorinids can be extended in the absence of a suitable substrate for settlement, as shown by observations on the temperate *Littorina littorea* by Thorson (1946). It is notable that both *Littoraria* species occur frequently on driftwood on the shore, so that rafting of adults is another potential means of transport (Jokiel, 1990; Ó Foighil, et al., 1999). However, human transport of the *Littoraria* species cannot be entirely ruled out. An example of apparent human introduction of a similarly large littorinid to the TEP is the record of a colony of the western Atlantic *Cenchritis muricatus* in the Gulf of California (Bishop, 1992; Chaney, 1992). For the minute *Peasiella conoidalis*, which was not collected alive or in its natural habitat, does not occur on driftwood, and was found on the American mainland rather than on the oceanic islands, the means of transport to the TEP (and indeed the validity of the record) are still less clear.

One puzzling aspect of the increasingly numerous reports of IWP species appearing in the TEP is that the immigrants seldom appear to become established as self-sustaining populations. Furthermore, those that do so apparently do not generally survive to become genetically differentiated (or specifically distinct) from their IWP ancestors, so that the evolutionary importance of trans-Pacific dispersal is limited (Vermeij, 1990). The reasons for the apparent failure of IWP species to become established are debated, and may include temporal instability of sea temperature due to ENSO events, limited availability of suitable habitat (especially of reefs and oceanic islands), and possible competition with the indigenous biota (Vermeij, 1990; Emerson, 1991; Glynn & Ault, 2000). The restriction of records of many IWP immigrant species to the islands of the TEP (and absence from the continental mainland) may further be explained by the prevailing westward-flowing currents between islands and mainland (Zinsmeister & Emerson, 1979). The difficulty of establishment faced by a planktotrophic species as a consequence of its type of development should also not be underestimated. As pointed out by Johannesson (1988), such species may disperse over long distances, but the density of recruits to a small founding population in the next generation is likely to be too low to sustain the population, since eggs and larvae will be swept away. Ironically, it may be that species without pelagic stages have a better chance of successful colonization since recruits remain close to their parents. However, oceanic islands can nevertheless support self-sustaining populations of planktotrophic species, since larvae can be retained in local circulation patterns (Scheltema et al., 1996).

In a discussion of the biogeography and classification of the only other trans-Pacific littorinid, *Littoraria pintado*, Reid (1999a) suggested that genetic contact between populations in the IWP and TEP was most unlikely and that their consistent difference in shell color might be evidence of genetic differentiation, thus justifying their classification as distinct subspecies. The present new records of likely natural transport across the EPB do not alter this conclusion. In contrast to the three species recorded here, *L. pintado* is not known to occur in the Line Islands and furthermore occurs as large self-sustaining populations on the TEP islands. The closest IWP populations of *L. pintado* occur in the Hawaiian Islands that lie in the weak westward-flowing North Equatorial Current; although this may transport some fish species from the TEP to Hawaii (Robertson & Allen, 1996) it has not been indicated as a route for trans-Pacific mollusks.

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